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MORPHOLOGICAL AND BEHAVIOURAL ASPECTS OF FEEDING IN THE CASSIDAE (TONNACEA, MESOGASTROPODA)

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ABSTRACT

Anatomy of the feeding apparatus, properties of the proboscis gland secretion, diet, and feeding behaviour of the Cassidae are reviewed from published data. New data are presented on the alimentary morphology of *Cassis tuberosa* and on the pursuit, attack, prey penetration and feeding methods of *C. tuberosa* and *Cypraecassis testiculus*. Tonnacean proboscis gland (PG) secretion is compared with accessory boring organ (ABO) secretion of the Naticidae and Muricidae.

The Cassidae are mainly nocturnal predators that feed specifically on echinoids; diets probably reflect the availabilities of specific echinoids in the habitat. The basic design of the alimentary system is similar to that of other tonnacean families. Two large proboscis glands deliver a secretion rich in sulfuric acid (pH < 1) via long ducts that pass through the nerve ring, along the proboscis to the buccal cavity. Prey are gripped by the foot and penetration of the test is achieved within about 10 min by the combined action of sulfuric acid and the radula. Scanning electron micrographs reveal severe etching, but no radular marks, on the cut edges of the test. Prey do not appear to be anaesthetized during attack. Consumption of internal tissue takes about 1–2 hr, but the feeding time can be more than doubled when all external tissue and spines are eaten. There appears to be no size selection of prey.

ABO secretion of naticids and muricids, which drill bivalves, and tonnacean PG secretion both dissolve minerals with the aid of an inorganic acid and probably a chelating agent. PG secretion, however, is much more acidic and is produced in far greater quantities than ABO secretion, and may lack the ability of the latter to attack the organic matrix of calcareous skeletal material prior to mineral dissolution.

INTRODUCTION

The beautiful shells of the Cassidae (helmet shells) have attracted attention almost to the total exclusion of the living animals. Yet these mesogastropods, which have a world-wide distribution in tropical to warm temperate sand and reef habitats, are intriguing not only because of their shells, but also because they feed almost exclusively on echinoids. In spite of this rather bizarre diet tor a gastropod, accounts of the feeding biology of cassids were, until recently, confined to brief notes scattered in various journals. In the present paper, we have synthesized information from the literature and present new data on the feeding methods of the Cassidae. Where relevant, we have also included published information on the Cymatiidae, Bursidae and Tonnidae that together with the Cassidae and Ficidae comprise the superfamily Tonnacea. Our review deals sequentially with the anatomy of the feeding apparatus, properties of the associated glands and their secretions, mode of attack, penetration and consumption of prey.

ANATOMY

The general plan of the alimentary system is similar throughout the Tonnacea, useful recent accounts being those of Day (1969) for *Argobuccinum,* and Houbrick & Fretter (1969) for *Cymatium* and *Bursa.* Reynell's (1905) anatomical description of *Galeodea (= Cassidaria) rugosa* (L.) suffers from poorly reproduced diagrams. The description of the cassid alimentary system given here is based on new data for *Cassis tuberosa* (L.) (Fig. 1a, b).

Proboscis and buccal apparatus

The mouth and buccal mass lie at the tip of the proboscis (Fig. 1, P) which, when fully ex-

tended, is 1 to 1.5 times the length of the shell, and when retracted lies within the proboscis sheath whose entrance forms a false mouth or rhynchodeum (RH). Retractor muscles running longitudinally in the proboscis wall become free in the proximal region of the proboscis, forming strap-like connections (PRM) with the walls of the cephalic haemocoel (CH). Retraction of the proboscis therefore involves both shortening, due to contraction of muscles in the proboscis wall, and inversion of the proximal region due to contraction of the free retractor muscles. The Cymatiidae lack free retractor muscles, and retraction occurs solely by contraction of the proboscis wall (Day, 1969; Houbrick & Fretter, 1969). The tonnacean proboscis is therefore rather different from the pleurembolic type of most neogastropods, where retractor muscles lying freely within the proboscis cavity are inserted along the length of the buccal mass (Day, 1969). The bulk of the retracted proboscis and the huge proboscis glands are compensated by reductions in the pallial organs in the anterior half of the pallial cavity. The hypobranchial gland becomes thin towards its anterior end and the anus is posi-

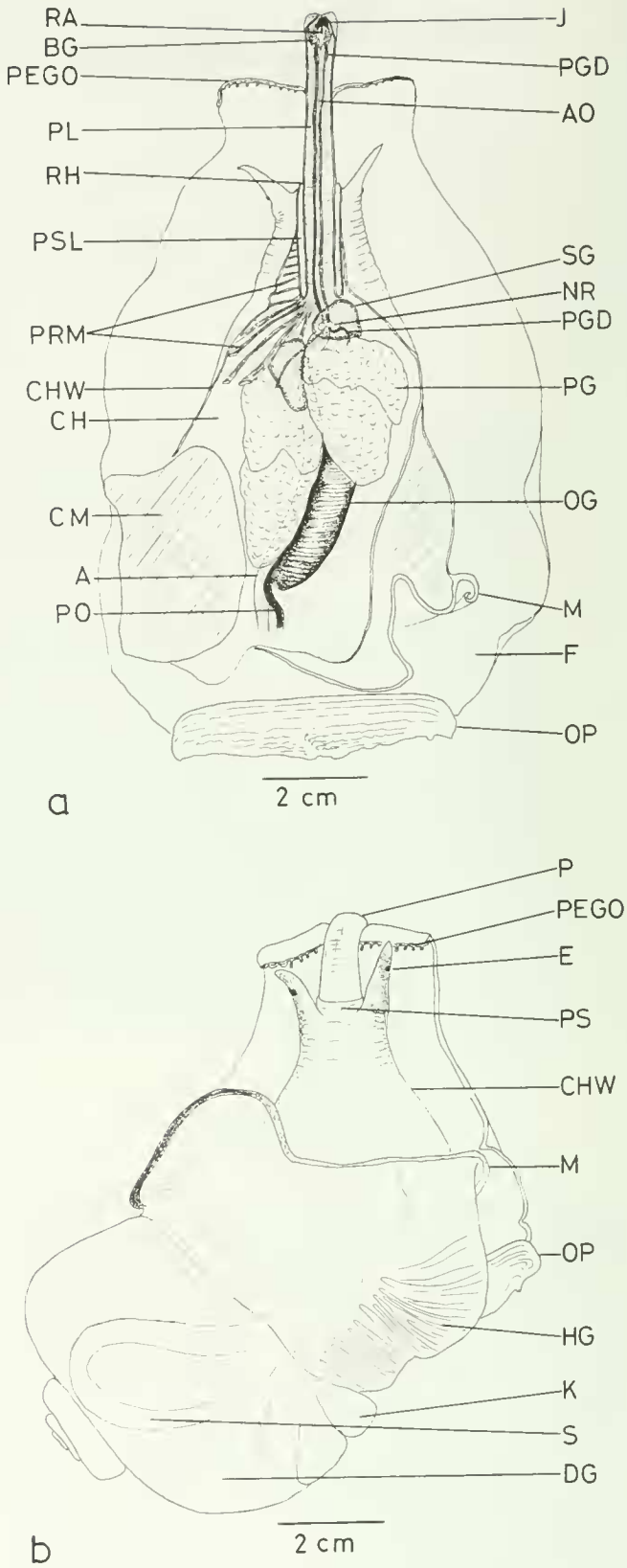
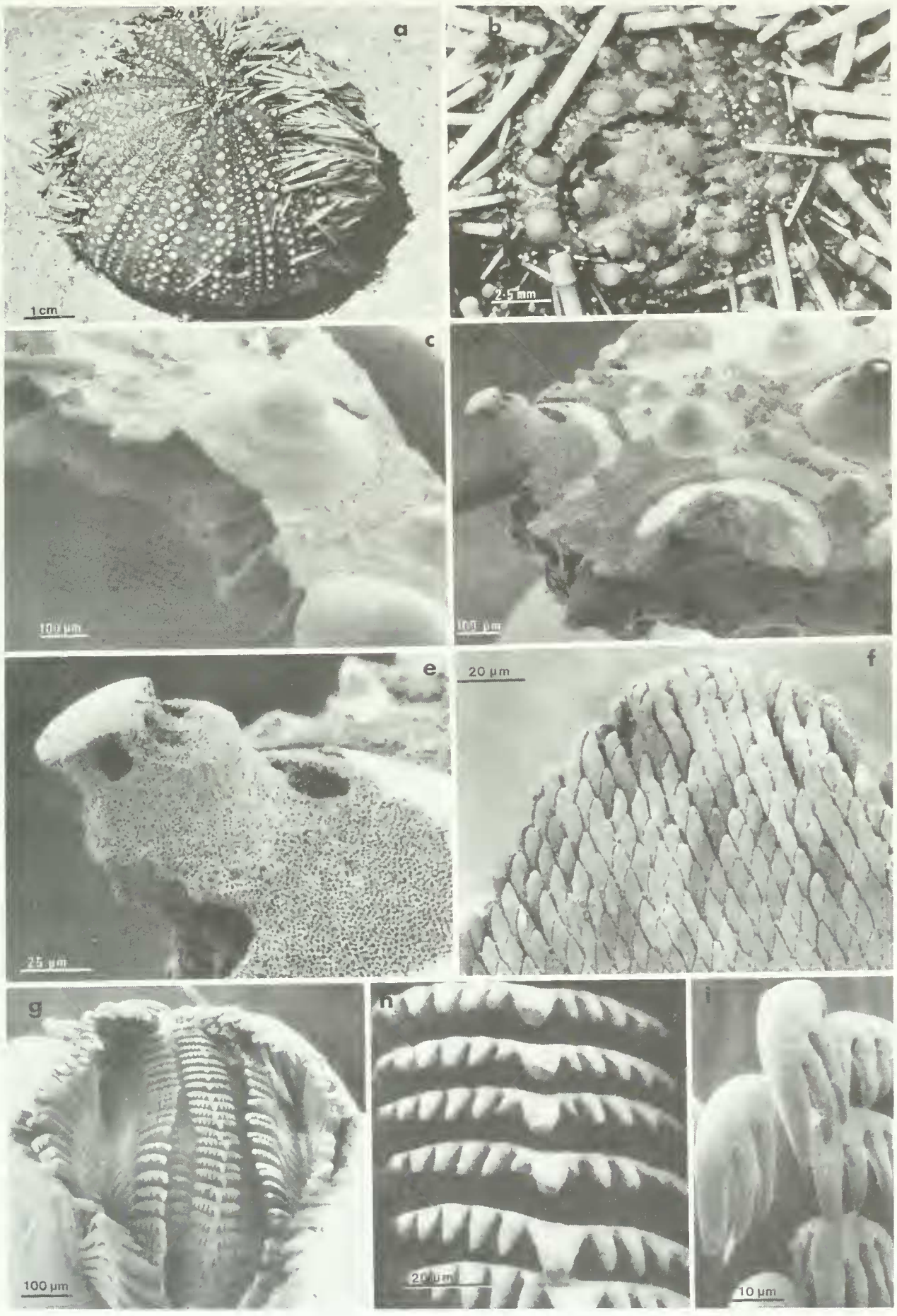


FIG. 1. **a.** *Cassis tuberosa*. The visceral mass, mantle and dorsal wall of the cephalic haemocoel have been removed to reveal the feeding apparatus and associated glands. A aorta, AO anterior esophagus, BG buccal gland, CH cephalic haemocoel, CHW cephalic haemocoel wall, CM columella muscle, F foot, J jaw, M mantle, NR nerve ring, OG esophageal gland, OP operculum, PEGO pedal gland opening, PG proboscis gland, PGD proboscis gland duct, PL proboscis lumen, PO posterior esophagus, PRM proboscis retractor muscle, PSL proboscis sheath lumen, RA radula, RH rhynchodeum, SG salivary gland. **b.** *Cassis tuberosa* removed intact from its shell. DG digestive gland, E eye, HG hypobranchial gland, K kidney, P proboscis, PS proboscis sheath, S stomach; other symbols as for Fig. 1a.

FIG. 2. **a.** *Tripneustes ventricosus* drilled by *Cassis flammea*, which had swallowed half the spines; **b.** *T. ventricosus* drilled by *Cassis tuberosa*. An area of spines has been cleared and a hole made in the test by cutting out a disc, which can be seen still in place. This urchin was removed from the *C. tuberosa* 10 min after the initial attack; **c.** Edge of hole in (b), showing undercutting caused by erosion by sulfuric acid; **d.** edge of disc showing severe etching by sulfuric acid; white areas are unetched surface material; **e.** higher magnification of spine boss in (d), showing severe etching; **f.** jaw of *Cassis flammea*; **g.** radula of *Cassis tuberosa*; **h.** central (rachidian) teeth showing wear on median cusps; **i.** marginal teeth; **c–i** are scanning electron micrographs.


a
1 cm
b
2·5 mm
c
100 µm
100 µm
e
25 µm
20 µm
f
g
100 µm
h
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tioned much further back than in other mesogastropod superfamilies.

The buccal mass, anchored within the tip of the proboscis by fine radiating muscles, contains a pair of horny jaws (J), the radula (RA) and associated odontophore, a region of glandular tissue (BG) behind the odontophore, and the openings of the paired proboscis gland ducts. Each jaw forms a bluntly pointed plate comprised of rows of contiguous rods, the distal ends of which form diamond-shaped subunits, giving the outer surface of the jaw a 'snake-skin' appearance. Instead of having a sharp saw-toothed edge as in *Cymatium* or *Charonia,* the jaw of *Cassis* has a blunt, rounded edge suitable for gripping spines and strands of flesh (Fig. 2f).

The radula has 7 teeth per transverse row, comprised of a central (rachidian) tooth on either side of which are a lateral and two marginal teeth (Fig. 2g). The central and lateral teeth are heavily cusped (Fig. 2h), whereas the marginal teeth are more delicately armed with 3 to 4 cusps arranged to form a claw (Fig. 2i). Ontogenetically, the marginal teeth become functional before the central and lateral teeth, and are used to grip shreds of flesh by intermeshing as the radula rolls backwards over the bending plane of the odontophore. More distally along the radula, the central and lateral teeth are used to rasp the calcareous tests of urchins, as a consequence of which their cusps become worn (Fig. 2h) and the delicate marginal teeth become torn away.

The buccal glandular tissue (BG) may be homologous to the "partly paired buccal gland" described in *Argobuccinum argus* (Gmelin) by Day (1969), to the "glandular patches" described in *Bursa granularis* (Röding) by Houbrick & Fretter (1969) and to the "blindsack" of *Tonna galea* (L.) (Weber, 1927). These glandular structures are of unknown function. Also opening into the buccal cavity are the paired proboscis gland ducts that deliver a secretion rich in sulfuric acid used to etch the calcium carbonate tests of urchins (Fig. 2 c–e).

Alimentary canal

On leaving the buccal mass, the anterior esophagus (Fig. 1a, AO) forms a narrow tube with dorsal and ventral typhlosoles, and runs along the proboscis, finally dropping sharply downwards through the nerve ring (NR). On emerging from the nerve ring, the esophagus immediately bends dorsalwards, whereupon its upper side is modified into the septate esophageal gland (OG), which runs alongside the aorta (A) beneath the proboscis glands (PG), almost for the remaining length of the cephalic haemocoel. The repeated transverse folds of the esophageal gland are richly supplied with secretory cells that in *Argobuccinum argus* are of three types, one secreting mucus and the others secreting unidentified digestive enzymes (Day, 1969).

The posterior esophagus (PO), which is a simple ciliated tube with thick muscular walls, leaves the esophageal gland and opens into the U-shaped stomach (Fig. 2b, S). The large digestive gland (DG) is connected to each limb of the stomach by separate ducts. The short intestine emerges, without sharp distinction, from the stomach and runs forward through the kidney sac (K) to the muscular rectum and anus.

Proboscis glands

The proboscis gland ducts (Fig. 1a, PGD) run from the buccal mass along either side of the esophagus, through the nerve ring, to the relatively massive glands lying in the cephalic haemocoel. This anatomical feature is unique to the Tonnacea. Each proboscis gland consists of 2 to 3 lobes, the right gland being considerably smaller and placed more centrally and further forward than the left gland beneath it (Fig. 1a). The proboscis glands are covered by an intricate network of muscles, the contraction of which forces the secretion through the proboscis gland ducts into the buccal cavity. The glands are anchored by fine muscle strands connecting to the body wall and foot.

The proboscis gland's histology has been described by Nüske (1973) for *Galeodea (= Cassidaria) echinophora* (Lamarck) and by Day (1969) for *Argobuccinum argus.* The following account is synthesized from both sources. Each gland consists of numerous tubules draining into collection ducts (Fig. 3a). The tubule walls are made of a single layer of large cells that produce the acid secretion (Fig. 3b). Nüske (1973) recognized three phases of cellular secretion. During secretion formation, large vacuoles are formed in the apical cell region by confluence of smaller vacuoles appearing to originate from the Golgi apparatus. The cells increase in size and attain a smooth boundary at the lateral and basal sides where they were previously

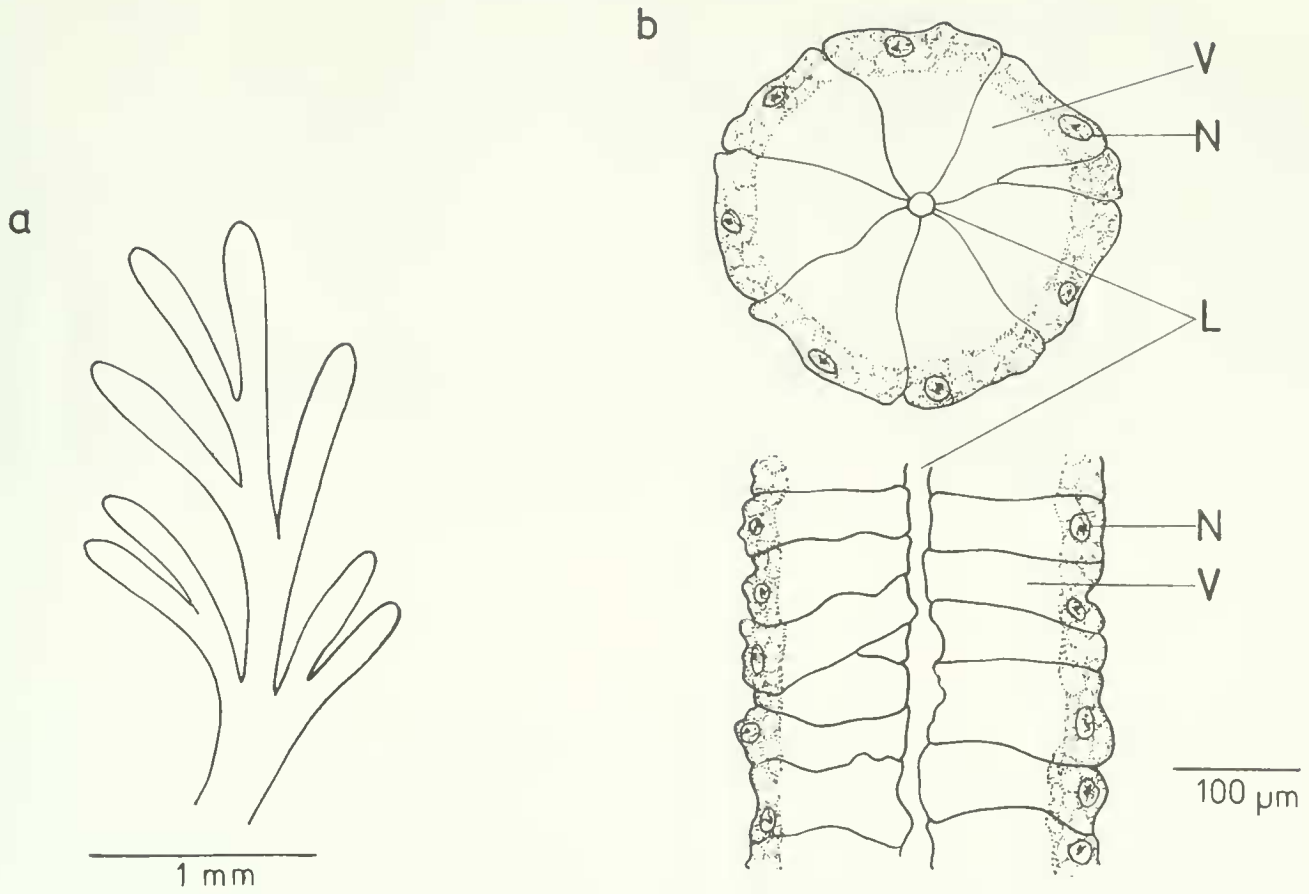

FIG. 3. **a.** dissected tubules of proboscis gland of *Argobuccinum argus* (after Day, 1969); **b.** transverse and longitudinal sections of PG tubules of *Galeodea echinophora* (after Nüske, 1973). L tubule lumen, N nucleus, V secretion vacuole.

thrown into interdigitating folds. These folds may represent a plasma membrane reservoir for the enlargement of the cells during secretion formation. When full, the cells are each occupied by one or a few large secretion vacuoles. The nucleus, cytoplasm, organelles and abundant small vacuoles are confined to the basal layer (Fig. 3b). After liberation of the apical secretion vacuole, the cytoplasm, containing numerous small vacuoles, becomes evenly spread throughout the entire cell. Meanwhile the cells shrink and become extensively folded along their lateral and basal sides. New secretion vacuoles appear within a few hours after the proboscis glands have been emptied (Nüske, 1973).

Proboscis gland secretion

The chemical properties of the proboscis gland secretion have been studied for *Galeodea echinophora* by Fänge & Lidman (1976) and for the cymatiid *Argobuccinum argus* by Day (1969), these recent analyses agreeing closely with the much earlier study of Panceri (1869) on *Tonna galea* and *G. echinophora*. The proboscis gland secretion of *G. echinophora* is hypertonic to seawater, with a pH of about 0.13. Hydrogen and sulfate ions are the predominant components, while sodium and chloride concentrations are lower than in the blood, and potassium and magnesium concentrations equal those in seawater. Only minute traces of organic material are present, and in this respect the Cassidae may differ from the Cymatiidae and Bursidae that are known to secrete toxins that anaesthetize the prey (Asano & Itoh, 1960; Day, 1969; Houbrick & Fretter, 1969). The secretion of the cymatiid, *A. argus,* has a pH of 1.1, and consists largely of 0.4–0.5 N sulfuric acid. Day (1969) established that the secretion contains no enzymes involved with the dissolution of calcium carbonate, but that 33% of the calcium carbonate (bivalve shell) dissolved by experimentally administered secretion was attacked by some component other than sulfuric acid, probably a chelating agent. How the proboscis gland cells store the strongly acid secretion without cellular damage, and the nature of the physical-chemical pathways which produce such high concentrations of hydrogen and sulfate ions, remain unknown.

TABLE 1. Recorded prey of the Cassidae.

Predator	Prey type	Prey species	Locality	Authority
Cassis tuberosa (L.)	epifaunal echinoids	*Tripneustes ventricosus* (Lamarck)	Florida Keys	Moore, 1956
			aquarium, Florida	Work, 1969
			aquarium, Barbados	Hughes & Hughes, 1971
			Barbados	present study
		Lytechinus (=Toxopneustes) variegatus (Lamarck)	aquarium, Bimini, Bahamas	Robertson quoted by Abbott, 1968a
			Florida	Lyman, 1937
		Diadema antillarum (Philippi)	Virgin Islands	Schroeder, 1962
				Gladfelter, 1978
			aquarium, Florida	Work, 1969
			Bimini, Bahamas	Snyder & Snyder, 1970
		Echinometra lucunter (L.)	aquarium, Barbados	Hughes & Hughes, 1971
			aquarium, Florida	Work, 1969
		Arbacia sp.	aquarium, Florida	Work, 1969
	burrowing echinoids	*Cassidulus caribboearum* Lamarck	Virgin Islands	Gladfelter, 1978
		Clypeaster rosaceus (L.)	Bimini, Bahamas	Foster, 1947
		Clypeaster subdepressus (Gray)	aquarium, Florida	Work, 1969
		Mellita quinquiesperforata (Leske)	aquarium, Florida	Work, 1969
		Echinoneus sp.	aquarium, Florida	Work, 1969
		Moira sp.	aquarium, Florida	Work, 1969
		Plagiobrissus grandis (Gmelin)	aquarium, Florida	Work, 1969
		Meoma ventricosa (Lamarck)	aquarium, Florida	Work, 1969
Cassis madagascariensis (Lamarck)	epifaunal echinoids	*Lytechinus (=Toxopneustes) variegatus* (Lamarck)	Florida	Lyman, 1937
	burrowing echinoids	*Plagiobrissus grandis* (Gmelin)	Florida Keys, unspecified locality	Moore, 1956, Chesher, 1969
		Meoma ventricosa (Lamarck)	Caribbean, unspecified locality	Chesher, 1969
Cassis flammea (L.)	epifaunal echinoids	*Echinometra lucunter* (L.)	aquarium, Barbados	Hughes & Hughes, 1971
		Tripneustes ventricosus (Lamarck)	aquarium, Barbados	Hughes & Hughes, 1971
	burrowing echinoid	unidentified spatangoid	Barbados	present study (circumstantial evidence)

Cassis cornuta (L.)	epifaunal echinoid	*Diadema setosum* (Leske)	Barrier Reef, Australia	Endean, 1972, 1973
	asteroid?	*Acanthaster planci* (L.)	Barrier Reef, Australia	Endean, 1969 (unsubstantiated report)
Cassis tessellata (Gmelin) (= *C. spinosa* Gronovius)	asteroid	*Oreaster clavatus* Muller & Troschel	aquarium, Ghana	Edmunds & Edmunds, 1973
Cypraecassis testiculus (L.)	epifaunal echinoids	*Lytechinus (=Toxopneustes) variegatus* (Lamarck)	Florida Panama	Lyman, 1937 Hendler, 1977
		Echinometra lucunter (L.)	aquarium, Barbados aquarium, Florida Panama	present study McPherson, 1968 Hendler, 1977
		Echinometra viridis Agassiz	Panama	Hendler, 1977
		Tripneustes ventricosus (Lamarck)	aquarium, Barbados	present study
		Diadema antillarum (Philippi)	aquarium, Barbados	present study
		"wide variety" of unspecified echinoids	aquarium, Florida	Work, 1969
		Eucidaris tribuloides (Lamarck)	aquarium, Florida Panama	Work, 1969 Hendler, 1977
	burrowing echinoids	*Echinoneus cyclostomus* Leske	Panama	Hendler, 1977
		Brissus unicolor Agassiz	Panama	Hendler, 1977
Cypraecassis rufa (L.)	epifaunal echinoids	*Tripneustes (= Toxopneustes) pileolus* (Lamarck)	Addu Atoll, Maldives	Taylor, 1978 (circumstantial evidence)
			Maziwi Island, Tanzania	Yaninek, 1978
		unspecified "short spined" sea urchins	East Africa	Spry, quoted by Abbott, 1968a
Cypraecassis coarctata (Sowerby)	epifaunal echinoid	*Echinometra vanbrunti* A. Agassiz	Sayulita, Mexico	Boone, personal communication
Phalium granulatum (Born)	burrowing echinoids	*Mellita quinquiesperforata* (Leske)	Florida Keys	Moore, 1956
		Cassidulus caribboearum Lamarck	Virgin Islands	Gladfelter, 1978 (circumstantial evidence)
Phalium labiatum (= zeylanicum) (Lamarck)	burrowing echinoid	*Echinodiscus bisperforatus* (Leske)	South Africa	Day, 1969
	bivalves?	unspecified (may be speculative)	South Africa	Day, 1974
Phalium bisulcatum (Schubert & Wagner)	burrowing echinoid	*Rhinobrissus hemiasteroides* A. Agassiz	Eniwetok lagoon	Kenzler, quoted by Abbott, 1968a (circumstantial evidence)
Phalium semigranosum (Lamarck)	bivalves?	unspecified (may be speculative)	Australia	Macpherson & Gabriel, 1962 cited by Abbott, 1968

Salivary glands

Partially embedded in the anterior lobe of each proboscis gland is a much smaller acinar salivary gland (Fig. 2a, SG). It has commonly been assumed that the salivary glands empty into the proboscis gland ducts, but Day (1969) found that the salivary glands of *Argobuccinum argus* empty directly into the esophagus immediately before the esophageal gland. Nüske (1973) described the salivary gland of *Galeodea echinophora* as consisting of mucus-secreting cells and "canaliculi" cells. The latter are characterized by intercellular canaliculi densely filled with microvilli and cilia, and Nüske (1973) suggested that they may produce the chloride component of the secretion emptying into the buccal cavity. This interpretation would seem to be erroneous if, as in *A. argus,* the salivary glands of cassids empty by separate ducts into the esophagus. Moreover, Fänge & Lidman (1976) found chloride to be present only in low concentrations in the secretion ejected from the proboscis of *G. echinophora.* Day (1969) claims that the salivary glands of *Argobuccinum argus* have a high amylase activity.

THE DIET

Records of prey taken by cassids are summarized in Table 1, from which it is evident that with very few exceptions, the Cassidae feed exclusively on echinoids. The exceptions are as follows. *Morum oniscus* (L.), not listed in Table 1, failed to eat any kind of echinoderm when an exhaustive series was offered in the laboratory (Work, 1969). *Cassis cornuta* (L.) was reported by a shell collector to eat the crown of thorns starfish *Acanthaster planci* (L.) (cited in Endean, 1969), and presumably this was the origin of Profant's (1970) claim that *C. cornuta* eats *A. planci.* Endean (1973), however, thought that the observer may have mistaken the urchin *Diadema setosum* (Leske) (known prey of *C. cornuta*) for *A. planci. Cassis tessellata* (Gmelin) (= *C. spinosa* Gronovius) "rasped away" at the astreroid *Oreaster clavatus* Muller & Troschel in captivity (Edmunds & Edmunds, 1973), but the success of this feeding attempt was not reported and the incident may have been induced by artificial conditions in the aquarium. *Phalium labiatum* (Lamarck) and *Phalium semigranosum* (Lamarck) are both reputed to feed on bivalves. The molluscan diet of *Phalium* is unsubstantiated and the reports may be speculative, since bivalves are common in the sandy areas populated by those cassids. *Phalium* spp. might be capable of drilling bivalve shells since the secretion of the cymatiid *Argobuccinum argus* etches *Macoma* sp. shells (Day, 1969). Nevertheless, bivalves have not been recorded in the diet of the better known species *Phalium granulatum* (Born).

A wide range of echinoids is consumed by the Cassidae, and diets seem to reflect the common species of urchin present in the habitat. Only stout-spined urchins such as *Eucidaris tribuloides* (Lamarck) tend to be avoided, although this species has been recorded in the natural diet of *Cypraecassis testiculus* (Hendler, 1977) and is readily taken by the cymatiid *Charonia variegata* Lamarck (McPherson, 1968; Work, 1969). Cassids living on sea-grass beds or near reefs feed on epifaunal echinoids, whereas populations of the same species living on soft substrata feed on burrowing echinoids. *Phalium* spp. always inhabit sandy substrata where they feed on burrowing echinoids, notably clypeastroids. Possibly, individuals become conditioned to specific echinoid prey. In the present study, *Cassis tuberosa* fed readily in the laboratory on *Tripneustes ventricosus* (Lamarck) and *Echinometra lucunter* (L.), but ignored *Diadema antillarum* (Philippi). However, Schroeder (1962), Snyder & Snyder (1970) and Gladfelter (1978) recorded *C. tuberosa* feeding on *D. antillarum* in the field. Of four *C. testiculus* (L.) that we collected from a single locality in Barbados, one fed rapaciously on *D. antillarum,* whereas the other three readily attacked *T. ventricosus* and *E. lucunter* but would not attack *D. antillarum.* However, they occasionally fed communally on *D. antillarum* that had been overcome by the first *C. testiculus.* Perhaps the technique of attacking the active, long-spined *D. antillarum* has to be learned.

Diets of newly settled or newly hatched cassids are unknown. They may feed on very small juvenile echinoids, but it is possible that they subsist on other, more readily available, invertebrate taxa.

On three occasions in the laboratory, *Cassis tuberosa* were seen to stop hunting and to twist the head back along the side of the shell aperture, extending the proboscis to reach the highest parts of the shell (Fig. 4d). The proboscis plucked at the shell surface as if to remove the algae growing there. The pur-

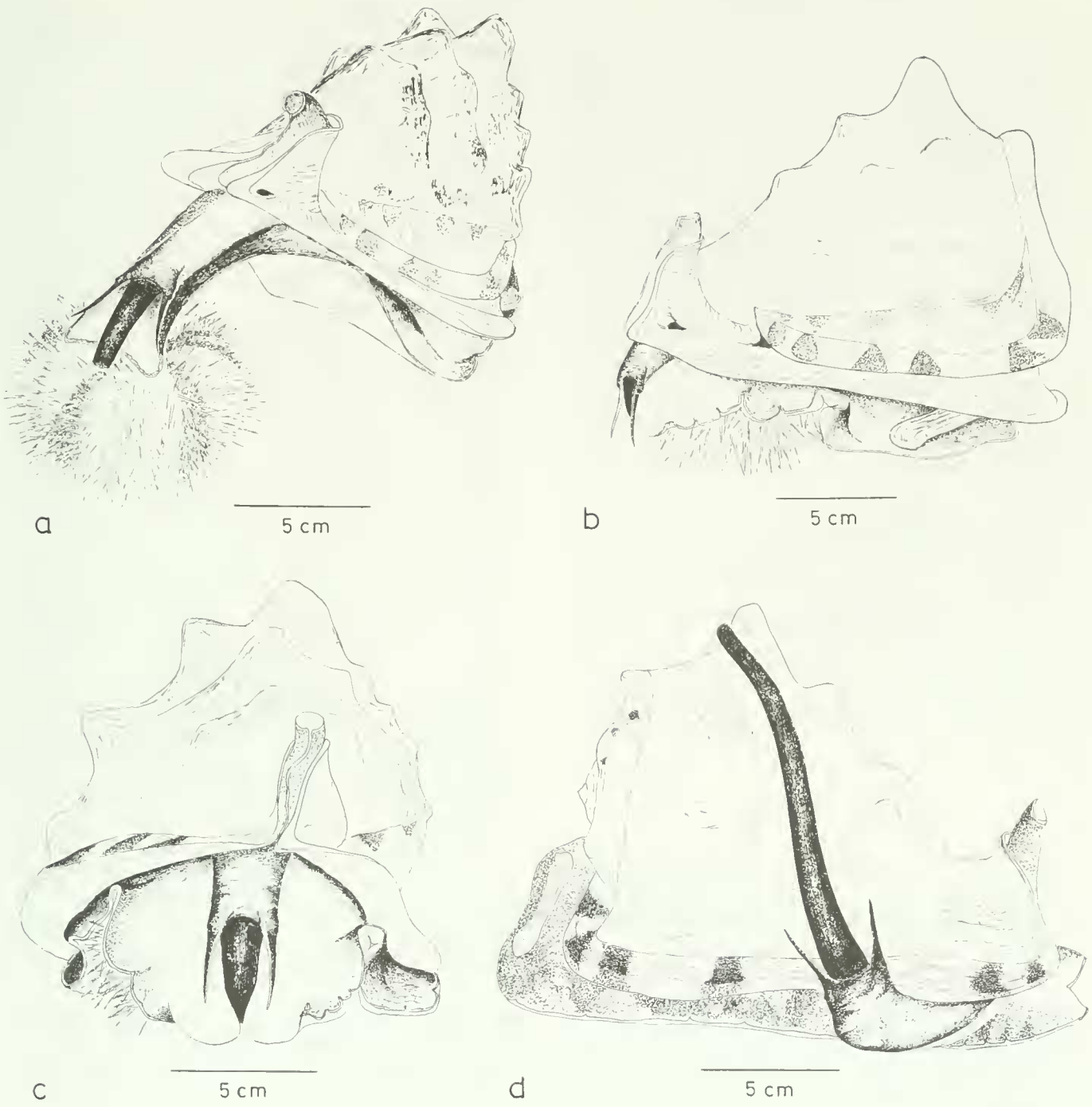

FIG. 4. **a.** *Cassis tuberosa* arching over *Tripneustes ventricosus* in initial phase of attack; **b.** urchin grasped by front part of foot; **c.** a groove between lobes of foot supports proboscis during penetration and feeding; **d.** extension of proboscis to 'clean' shell surface.

pose of this behaviour remains a mystery, as removal of the algae would detract from the camouflage they provide; the possibility that the algae supply some essential nutrients, not available from the prey, seems unlikely.

FEEDING METHODS AND BEHAVIOUR

The following account of feeding methods is based largely on observations of 4 individuals of *Cassis tuberosa,* 1 of *C. flammea* (L.) and 4 of *Cypraecassis testiculus* collected in Barbados during April 1980. The animals were kept at about 29°C in a shallow concrete tank (3.95 m long and 0.76 m wide) filled to a depth of 18 cm with running seawater. The *C. testiculus* were partitioned off in an area of the tank and provided with a 4 cm layer of sand. Observations were made throughout the night using a dimmed torch.

Hunting behaviour

Cassis spp. and *Cypraecassis testiculus* seldom moved during daylight, remaining partially (*Cassis* spp.) and wholely (*C. testiculus*) buried in sand when it was available. Animals began feeding at various times throughout the night, but generally ceased feeding at daybreak. The single specimen of *Cassis flammea* was exceptional because, during the day, it often remained feeding on urchins that it had attacked the previous night. In contrast to these observations, Boone (personal communication) saw *Cypraecassis coarctata* (Sowerby) feeding on urchins during the day in the field. The typically nocturnal feeding habits of the Cassidae are paralleled by those cymatiids that feed on mobile prey (Houbrick & Fretter, 1969; Laxton, 1971). Diurnal feeding apparently occurs only in sluggish cymatiids that 'graze' on sedentary invertebrates (Laxton, 1971). While hunting, *Cassis tuberosa* moves steadily at a speed of about 0.3 cm per second, turning only gradually during its trajectory. The much smaller *Cypraecassis testiculus* moves at a speed of about 0.5 cm per second, with frequent erratic turns.

Method of attack

Cassis spp. and *Cypraecassis testiculus* have quite different attack methods. *C. tuberosa* detects prey by olfaction, and when it approaches to within a few cm of an urchin, the siphon bends forward and the tentacles become fully extended. Just before tentacular contact is made, the front edge of the foot is raised slightly. As soon as the tentacles touch the urchin, the front half of the foot is raised in a high arch so that the shell is inclined at an angle of about 30°. *C. tuberosa* continues to move forwards on the hind portion of its foot, at the same time extending its head over the urchin (Fig. 4a). During this maneuver, which usually takes less than 10 sec, no contact is made with the urchin except for very brief delicate touches by the tentacles. This is important, because most epifaunal urchins can move faster than *C. tuberosa* and would often escape if alarmed before they were covered by the predator. Such escapes were observed frequently in the laboratory, the urchins apparently alarmed by the scent of the approaching *C. tuberosa*. Snyder & Snyder (1970) however, found that *Diadema antillarum* were unresponsive to *C. tuberosa* placed upcurrent in the field, but reacted violently when touched by the predator. Schroeder (1962) maintained that in the field, pursuits of fleeing *D. antillarum* by *C. tuberosa* were usually successful.

When the urchin is adequately covered, *Cassis tuberosa* drops down on the prey, grasping it with the bilobed front portion of the foot (Fig. 4b). The lobes of the foot provide a secure hold on the urchin and the groove between them supports the proboscis during penetration and feeding. The proboscis is also supported during feeding by folds in the front edge of the foot in *Cypraecassis testiculus* (Fig. 5b, c), *Charonia* spp. (Laxton, 1971) and *Cymatium nicobaricum* (Röding) (Houbrick & Fretter, 1969). Schroeder's (1962) description of the attack behaviour of *C. tuberosa* feeding in the field on *Diadema antillarum* agrees with ours of *C. tuberosa* feeding on *Tripneustes ventricosus* and *Echinometra lucunter,* except that when feeding on *D. antillarum, C. tuberosa* repeatedly inserts its proboscis among the spines while arching over the prey. *D. antillarum* is a particularly agile urchin, and it is possible that *C. tuberosa* administers a toxin among the spines to hinder the urchin's retreat. It is uncertain, however, whether cassids are able to secrete toxins.

Our single specimen of *Cassis flammea* did not arch over its prey, but tried to mount urchins directly, with the result that many of them escaped. When successful, *C. flammea* gripped the side, or at most, only half the upper surface of the urchin with the front of its foot. This specimen of *C. flammea* was collected on a fine sand substratum where the only potential echinoid prey were spatangoids and clypeastroids. Although we could not induce the *C. flammea* to eat *Mellita quinquiesperforata* (Leske) or large *Meoma ventricosa* (Lamarck) in the laboratory, it is likely that it had been feeding on burrowing echinoids in the field; these prey may require a different attack method than epifaunal echinoids. Moore (1956) described how, when feeding on the large burrowing urchin *Plagiobrissus grandis* (Gmelin), *Cassis madagascariensis* (Lamarck) burrows downwards at a steep angle through the sand and clasps the echinoid in the front part of its foot. Moore (1956) also found *Phalium granulatum* feeding on *M. quinquiesperforata*; the predators were perched on top of their prey and had penetrated the test near the centre of the aboral surface. Kier (personal communica-

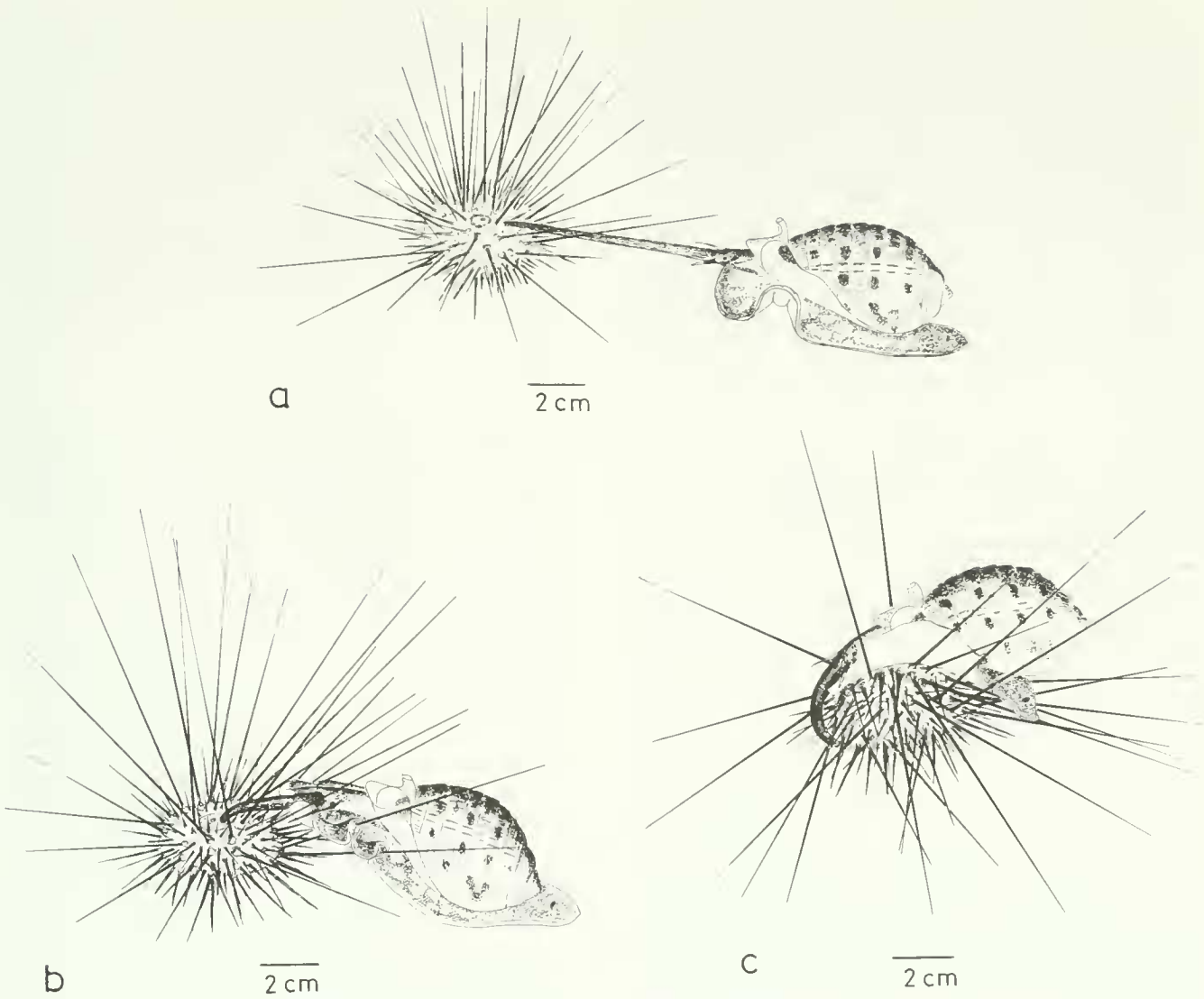

FIG. 5. **a.** *Cypraecassis testiculus* shooting out its proboscis in initial attack on *Diadema antillarum*; **b.** spines are gripped by front part of foot; **c.** *Cypraecassis* mounts urchin and commences feeding.

tion) recorded, by time lapse photography, the feeding of *P. granulatum* on the burrowing echinoid *Cassidulus caribboearum* Lamarck. After moving about the aquarium for several hours of the night, *P. granulatum* stopped and burrowed partially into the sediment. After 8 minutes a dead denuded *C. caribboearum* appeared at the surface and *P. granulatum* resumed locomotion. This represents an outstandingly rapid attack procedure that clearly deserves further study. The film also revealed that *C. caribboearum* sensed the approach of *P. granulatum* and responded by surfacing and moving away as fast as possible.

Cypraecassis testiculus is able to detect echinoids by olfaction from at least 30 cm downstream in a weak current. Once detected, the prey are approached swiftly and directly. On making first tentacular contact with *Tripneustes ventricosus* and *Echinometra lucunter, C. testiculus* extends its proboscis and applies it repeatedly to the test among the spines, penetration commencing within 1–2 min. Meanwhile, the spines are grasped by the forepart of the foot, and by the time penetration is well underway, *C. testiculus* has the urchin securely enveloped. Urchins under attack wave their tube feet and spines wildly, and *C. testiculus* is frequently dragged 30–50 cm before the prey becomes incapable of further locomotion.

Diadema antillarum elicits a rather different attack behaviour. When 1–2 shell lengths away from the urchin, *Cypraecassis testiculus* quickly shoots out its proboscis and applies it repeatedly to the periproct (Fig. 5a). The urchin invariably reacts by violently waving its spines and tube feet, retreating hastily. Often, *C. testiculus* is able to gain on the retreating *D. antillarum* and to grasp its spines with the front of the foot, whereupon the attack always succeeds (Fig. 5b, c). Sometimes

D. antillarum escapes before *C. testiculus* is able to grasp the spines. In the confines of the laboratory aquarium, a chase ensues that may involve several unsuccessful attacks, but usually ends in victory. The swift application of the fully extended proboscis when *C. testiculus* attacks *D. antillarum* is reminiscent of the probing action of the proboscis of *Cassis tuberosa* when it also attacks this species, again suggesting that a toxin is being delivered to hinder the retreat of such a mobile prey.

Secretion of toxins

The reputation of the Cassidae for secreting toxins derives both from inference, since certain other members of the Tonnacea are known to produce toxins, and from the experiments of Cornman (1963), who found that the secretion delivered from the proboscis of *Cassis tuberosa,* when diluted to 1/1000, would incapacitate the spines and tube feet of *Diadema antillarum* immersed in the solution. We examined the mobility of spines and tube feet of numerous urchins under attack from *Cassis* spp. and *Cypraecassis testiculus,* but could find no evidence for action of a toxin. Spines and pedicellariae remained active throughout the attacks, and remained active for some time even after all internal tissue had been eaten. The tube feet remained active and retained their ability to attach themselves to the substratum for at least 10 min after the initial attack, by which time penetration of the test was usually achieved. After this time, there was a tendency for the tube feet on certain ambulacra to curl up and lose their response to touch, while those on other ambulacra remained active. Internal examination of the tests showed that the ampullae had been stripped from those ambulacra with inactive tube feet.

It is still possible, however, that cassids produce a toxin that interferes with the coordination of the spines and tube feet, thus impeding locomotion without inhibiting their activity. Such a subtle effect would be hard to detect experimentally. By contrast, cymatiids and bursids such as *Argobuccinum argus* (Day, 1969), *Cymatium nicobaricum* and *Bursa* spp. (Houbrick & Fretter, 1969) produce toxins that have very marked anaesthetic effects on their prey. Moreover, the toxin produced by *Fusitriton (= Argobuccinum) oregonensis* (Redfield) has been identified as tetramethylammonium tetramine (Asano & Itoh, 1960). Cymatiid toxin appears to be secreted by the proboscis gland, as Laxton (cited by Endean, 1972) found that extract only from the posterior segment of the "salivary" gland of *Charonia rubicunda* (Perry) would paralyse starfish. Fänge & Lidman (1976), however, found only minute traces of organic material in the secretion of *Galeodea echinophora.* The ability of cassids to produce toxins thus remain open to question.

Role of mucus

While handling its prey, *Cassis tuberosa* secretes a thick layer of stiff mucus from the transverse slit along the front edge of the foot (Fig. 1a, b, PEGO). The prey's spines become flattened down, all facing away from the area of penetration, under the layer of mucus by gradual pressure from the predator's foot. In this way, the spines do not damage the snail. Pedicellariae become detached and trapped in the mucus, thereby rendered harmless. Copious quantities of mucus are also secreted by *Cypraecassis testiculus,* as a result of which the snail is able to climb onto its prey without damage from spines and pedicellariae. Mucus is an important agent in the attack method of other tonnaceans. *Cymatium nicobaricum* secretes a thick, resilient curtain of mucus over the aperture of its gastropod prey, thus forming a seal around the proboscis which is inserted into the lumen of the prey's shell (Houbrick & Fretter, 1969).

PENETRATION OF THE PREY

Position of penetration

Cassids usually penetrate their prey through the test, but sometimes entry is gained through the membranous peristome, or in the case of *Diadema antillarum,* through the periproct. The diameter of the hole made in the test reflects the size of the predator, being about 9 mm for adult *Cassis madagascariensis,* 5–6 mm for *C. tuberosa,* 3–4 mm for *C. flammea,* 2–3 mm for *Cypraecassis testiculus* and 1–3 mm for *Phalium granulatum.* Penetration may occur anywhere on the test, but some regions are penetrated more frequently than others. Hughes & Hughes (1971) found that *Cassis tuberosa* feeding on *Tripneustes ventricosus* and *Echinometra lucunter* penetrated about 50% of the urchins through the side, about 13%

through the top and about 13% through the base of the test. The rest were entered through the peristomeal membrane. When feeding on the burrowing echinoid *Cassidulus caribboearum, C. tuberosa* usually penetrates the relatively spine-free ventromedial region of the test, but this site-preference is lost when very small individuals are attacked (Gladfelter, 1978). Foster (1947) recorded a *C. tuberosa* penetrating the burrowing urchin *Clypeaster rosaceus* (L.) near the anal region, while Moore (1956) described a specimen of the large burrowing urchin, *Plagiobrissus grandis,* as having been penetrated through the anterolateral edge by *Cassis madagascariensis*. In the present study, *C. flammea* feeding on *T. ventricosus* and *E. lucunter* penetrated 6 urchins through the side, 3 through the top and 1 through the base of the test. *C. testiculus,* also feeding on *T. ventricosus* and *E. lucunter,* penetrated 15 urchins through the periostomeal membrane, 1 through the base of the test, 5 through the side and 7 through the top. Five *D. antillarum* were penetrated by *C. testiculus* through the periproct and 1 through the peristomeal membrane, but none was penetrated through the test. Because of its membranous periproct, *D. antillarum* is particularly vulnerable to attack in this region. Moore (1956) found 3 *P. granulatum* to have penetrated the clypeastroid *Mellita quinquiesperforata* near the centre of the aboral surface. Beu et al. (1972) observed that New Zealand Tertiary Spatangoida presumed to have been eaten by cassids or cymatiids, were drilled mainly near the anterior end of the test, and remarked that a predator holding the prey in an anterior position would prevent the prey escaping and would be able to push inside the backwardly directed spines more easily.

The bias of *Cypraecassis testiculus* to penetrate *Tripneustes ventricosus* and *Echinometra lucunter* through the periostomeal membrane contrasts with the tendency of *Cassis tuberosa* and *C. flammea* to penetrate these urchins through the side of the test. In all cases, the proboscis can easily be extended to all inner parts of the prey and the position of entry would seem to be correlated either with the way the prey is gripped during feeding (*Cassis* spp. feeding on *T. ventricosus* and *E. lucunter*) or with the ease of penetration (*C. tuberosa* feeding on *Cassidulus caribboearum, C. testiculus* feeding on *T. ventricosus, E. lucunter* and *Diadema antillarum*).

Mechanics of penetration

Before cassids penetrate the prey test, an area slightly larger in diameter than that of the proboscis is cleared of spines that are swallowed by *Cassis* spp. but, except for very small ones, discarded by *Cypraecassis testiculus. Cassis tuberosa* and *Cypraecassis testiculus* complete this phase in 4–5 min. A circular groove is then cut in the test, again taking about 5 minutes. The disc of test thereby cut out is usually pushed inwards, but sometimes is displaced outside the test. Cutting is achieved by the combined action of sulfuric acid and radula. Scanning electron micrographs reveal severely etched surfaces but no signs of radular scrape marks (Fig. 2c–e). The median cusps of the central teeth, however, show considerable wear (Fig. 2h), and the buccal mass of *C. testiculus* was seen to be in perpetual rhythmic action during penetration. The radula is thus undoubtedly used in the drilling process and probably removes the calcium sulfate produced during etching, thereby exposing new layers of calcium carbonate to the sulfuric acid and maximizing the rate of erosion. Day (1969) found that etching was impeded by the precipitate of calcium sulfate formed when drops of sulfuric acid were placed on bivalve shells. The radula must also be instrumental in rasping through the peristomeal and periproct membranes that are more resistant to the action of sulfuric acid than the test.

The etched surface of the test is confined to within a few μm of the edge of the hole (Fig. 2c), suggesting that the 'lips' of the proboscis form a seal around the area penetrated, thereby preventing leakage and dilution of the sulfuric acid. Considerable amounts of sulfuric acid may continue to be secreted after penetration because the plates of the test become loosened and the test is easily crushed. The delicate tests of *Diadema antillarum* are often crushed by the weight of *Cypraecassis testiculus* during feeding. Collapse occurs merely because the tests have been weakened by erosion and not, as suggested by Schroeder (1962), because the predator has crushed them with its foot to render the inner parts more accessible.

CONSUMPTION OF PREY

Having penetrated the test, *Cassis tuberosa, C. flammea* and *Cypraecassis testiculus*

consume all the internal tissue, leaving only the gut contents, the peristomeal membrane, and occasionally some of the ampullae. When the internal tissue has been eaten, *C. tuberosa* and *C. flammea* often commence to eat the tube feet, pedicellariae and spines, the proportion eaten varying widely and depending on the appetite. The spines are voided intact in the feces, stacked in parallel in bundles and intermingled with thin black filaments up to 30 cm long. *C. testiculus* swallows only the very smallest spines but eats the tissue and muslces at the bases of the larger spines that become detached and drop to the substratum. The long mobile spines of *Diadema antillarum* have very large basal muscles and these must comprise a relatively high proportion of the diet when this species is eaten.

Surprisingly, we found no significant correlation between the time taken to penetrate and consume an urchin (handling time) and the size of the prey (Fig. 6). Much of the variation in handling time was due to the proportion of spines eaten. Hughes & Hughes (1971) found that of 295 *Tripneustes ventricosus* and *Echinometra lucunter* eaten by *Cassis tuberosa,* about 30% had <9% spines eaten, 50% had 10–90% spines eaten, and 20% had 90–100% spines eaten. The mean handling time for *C. tuberosa* feeding on *T. ventricosus* and *E. lucunter* in the present study was 79 min, S.E. = 6.4 min, n = 38. The single *Cassis flammea* always consumed all the spines and took an average of 5.5 hr to finish each meal, whereas *C. tuberosa* seldom took more than 2.5 hr, even when all spines were eaten. In spite of its small size, *Cypraecassis testiculus* consumed *T. ventricosus* and *E. lucunter* at the same rate as *C. tuberosa,* the mean handling time being 79 min, S.E. = 9 min, n = 25.

Dietary value of prey and size selection

In order to estimate the dietary value of the internal and external tissue of *Tripneustes ventricosus, Echinometra lucunter* and *Diadema antillarum,* we dried samples of intact urchins and those preyed upon by *Cassis* spp. and *Cypraecassis testiculus* to constant

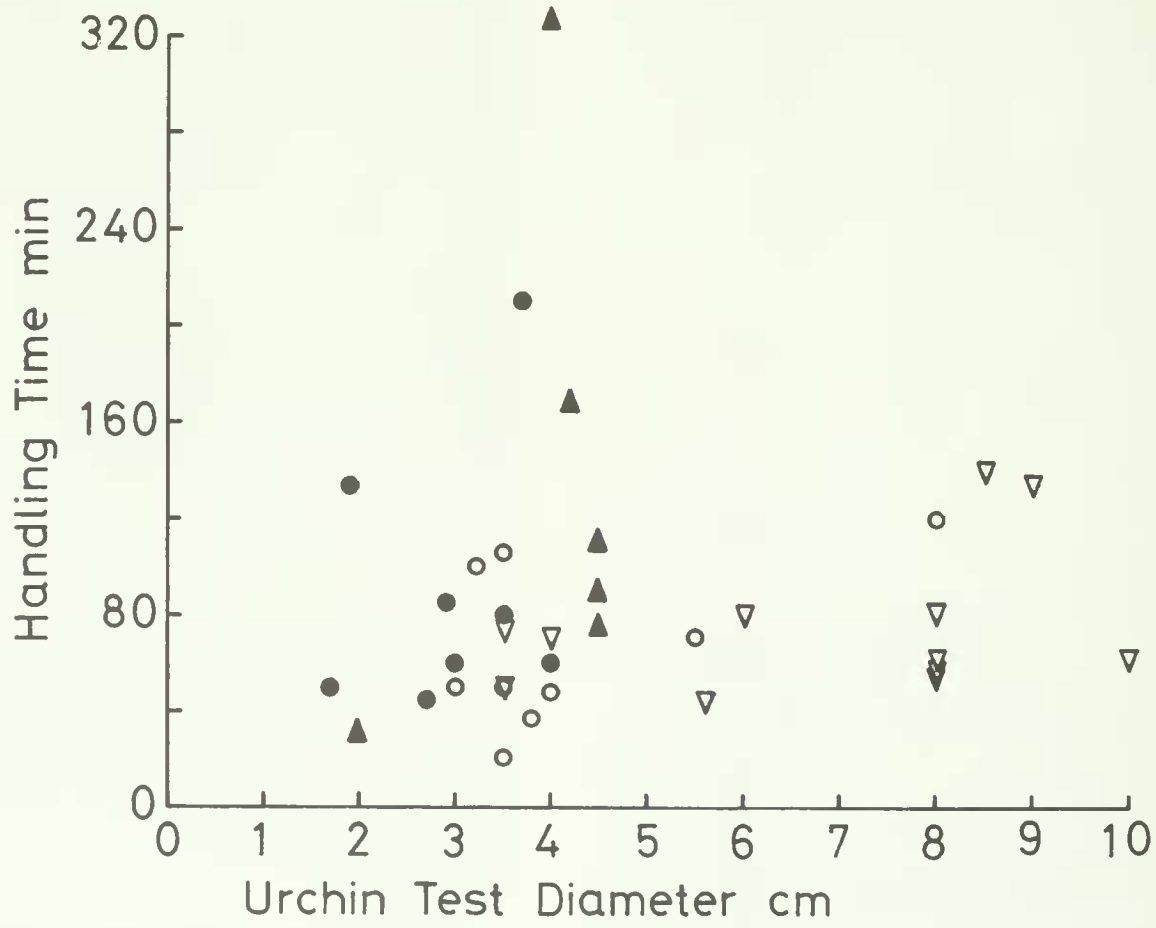

FIG. 6. Handling time (time taken to penetrate test and finish meal plotted against diameter (excluding spines) of prey; ▽ *Cassis tuberosa* feeding on *Tripneustes ventricosus*; ● *Cypraecassis testiculus* feeding on *Echinometra lucunter*; ○ *C. testiculus* feeding on *T. ventricosus*; ▲ *C. testiculus* feeding on *Diadema antillarum.*

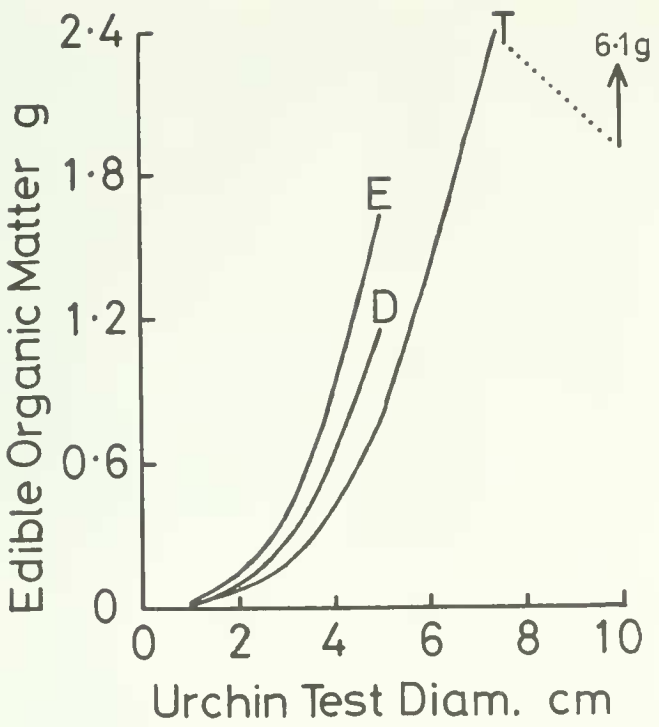

FIG. 7. Ash free dry weight of total edible organic matter as a function of diameter of prey. E *Echinometra lucunter,* D *Diadema antillarum,* T *Tripneustes ventricosus*. Regression equations for the data after $\log_e$ transformation of both variables are: E y = 2.8x − 3.5, T y = 3.0x − 4.5, D y = 2.9x − 3.6. Intercept values for internal edible organic matter are E − 4.0, T − 5.0, D − 4.5.

weight at 60°C, heated them in a muffle furnace for 3 hr at 500°C and reweighed them. Only urchins that had either all or none of the spines eaten were chosen. We estimated that the external tissue accounted for about 31% of the total ash free dry weight of the meal when all spines were eaten. The total ash free dry weight of edible material (internal plus external) increased approximately as the cube of the diameter (i.e. volume) of the test (Fig. 7). The nutritional value of an urchin will, of course, differ greatly according to whether its gonads are fully ripe, as in our material, or spent.

Since the time taken to penetrate urchins is only a small proportion of the total handling time, the dietary value of urchins would seem to increase monotonically with size. We should expect, therefore, that larger urchins would be preferred to smaller ones, as long as they can be caught easily. There is no evidence, however, for the size selection of prey by cassids. The most substantial data are for *Cassis tuberosa* feeding on *Cassidulus caribboearum* (Gladfelter, 1978). In this case, the size frequency of live urchins in the prey population was similar to that of tests cast up on the shore after being drilled by *C. tuberosa*.

At least in shallow water, cassids are usually nocturnal predators that retreat into the sand at daybreak to avoid predation. During the hours of darkness there is time to eat only a few urchins and, if the encounter rate with prey is low or uncertain, it may pay to attack the first urchin encountered, irrespective of size. This is a 'time-minimizing' as opposed to an 'energy maximizing' feeding behaviour (Hughes, 1980). In support of this interpretation, we found that on completing a meal, *Cassis tuberosa* and *Cypraecassis testiculus* would usually retreat into the sand until the following evening. Size selection of prey, suggesting an energy maximizing feeding behaviour has, however, been recorded in *Cymatium nicobaricum*, which prefers larger to smaller gastropods (Houbrick & Fretter, 1969). It is perhaps significant that this predator will continue feeding during the day, albeit less frequently, than at night.

DISCUSSION

The ability to drill through the calcareous plates and shells of echinoderms and mollusks has evolved independently in the Tonnacea, Naticidae and Muricidae. In the Naticidae and Muricidae drilling is achieved by alternating application of the accessory boring organ (ABO) and the radula to the excavation. The ABO, located in the propodium, secretes a mucoid, slightly acidic, hypertonic fluid rich in hydrogen, chloride and sodium ions. The ABO secretion also contains carbonic anhydrase and probably other enzymes and chelating agents (Carriker & Williams, 1978). Etching of the prey shell begins by the preferential dissolution of the organic matrix, probably by proteolytic enzymes, which has the effect of increasing the surface area of mineral crystals exposed to solubilization and facilitating the removal of shell material by the radula (Carriker, 1978). Minerals are dissolved by the hydrochloric acid and probably also by a chelating agent and the action of carbonic anhydrase. Calcium ions freed from the shell in the borehole enter the microvilli of the ABO and pass into the foot of the snail, the transmembrane flux of calcium probably being aided by carbonic anhydrase and adenosine triphosphate (Carriker & Williams, 1978).

The chemical etching process of the tonnacean proboscis gland (PG) secretion

resembles that of the naticid and muricid ABO secretion in that mineral dissolution involves an inorganic acid and probably a chelating agent (Day, 1969). PG secretion, however, is produced in much larger quantities than ABO secretion (large *Galeodea echinophora* can eject up to 1 ml of secretion when irritated [Fänge & Lidman, 1976], compared with the few μl secreted by the ABO of *Urosalpinx cinerea follyensis* Baker during excavation [Carriker et al., 1978]) and is more acidic (pH 0.13 in *G. echinophora* [Fänge & Lidman, 1976], pH 1.1 in *Argobuccinum argus* [Day, 1969], compared with ABO secretion of pH 3.8–4.0 when in contact with seawater in *U. cinerea* [Carriker et al., 1978]). PG secretion differs further from ABO secretion in having a high concentration of sulfate and a relatively low concentration of chloride ions, a much lower concentration of organic matter and an apparent lack of enzymes (Fänge & Lidman, 1976; Day, 1969). The in vitro calcium carbonate solubilizing properties of *A. argus* PG secretion are unimpaired by boiling the secretion (Day, 1969), whereas ABO secretion of *U. cinerea* loses its etching properties after heating to 80°C (Carriker & Williams, 1978).

Cassids penetrate echinoid test at a speed of about 0.1 mm per minute in contrast to the muricid *Urosalpinx cinerea* that penetrates oyster shell at a speed of about 0.3–0.5 mm per day (Carriker & Williams, 1978). Most of this difference in drilling speed is probably attributable to the porous structure of echinoid test (Fig. 2c–e) compared with the denser material of bivalve shell. This comparison, however, is complicated by the fact that cassids cut out a disc, whereas naticids and muricids bore a hole. The drilling speed of tonnaceans, if they could be induced to penetrate bivalve shells, would be of great interest. Day (1969) found that PG secretion of *Argobuccinum argus* had produced a shallow depression 2–3 hr after being placed on the valve of *Macoma* sp., but of course the calcium sulfate accumulating over the etched surface would have progressively retarded erosion. Day (1969) concluded that the mineral fraction was dissolved faster than the organic fraction of the shell because remnants of the organic matrix at the edges of the eroded area were visible under the microscope. If this interpretation is correct, the action of tonnacean PG secretion would contrast with that of naticid and muricid ABO secretion, which attacks the organic matrix prior to the dissolution of minerals.

The drilling of molluscan shells by tonnaceans has never been recorded with certainty. Molluscivorous cymatiids penetrate their prey through the shell apertures. *Cymatium nicobaricum* inserts its proboscis into the mantle cavity of its gastropod prey (Houbrick & Fretter, 1969) and *Monoplex australasiae* Perry pushes its proboscis down through the substratum and in between the valves of its bivalve prey (Laxton, 1971). Sulfuric acid, although adequate for corroding the porous plates and spicules of echinoderms, may not be as effective as ABO secretion of naticids and muricids for etching the more solid material of molluscan shells.

It is debatable whether the secretion of sulfuric acid by tonnaceans evolved first as a defensive or as an offensive device. Sulfuric acid would seem, a priori, not to be a particularly effective agent for attacking prey lacking calcareous armory, yet well developed sulfuric acid-secreting proboscis glands are possessed by all tonnaceans, even though many of them in the Cymatiidae and Bursidae feed on soft bodied prey such as polychaetes, sipunculans, ascidians and sponges (Houbrick & Fretter, 1969; Laxton, 1971; Taylor, 1978). Sulfuric acid may, however, be effective in overcoming soft-bodied prey. When feeding on the sabellariid polychaete, *Gunnarea capensis* (Schmarda), *Argobuccinum argus* inserts its proboscis into the worm's tube and ejects a secretion into the crown of flattened setae that protect the head of the prey. The setae become loosened and can be dislodged by the predator's radula. Further experiments are needed, of course, to determine whether enzymes are secreted in addition to the sulfuric acid.

Echinoderms predominate in the diets of tonnaceans; the Cassidae specialize on echinoids; the Tonnidae probably feed largely on holothurians (Bakus, 1973; Grange, 1974; Taylor et al., 1980), although Weber (1927) claimed that *Tonna galea* accepted echinoids; the Ficidae feed "on sea urchins and other echinoderms" (Abbott, 1968b), but actual data on ficid diets are lacking in the literature; the Bursidae feed on ophiuroids, echinoids and crinoids in addition to non-echinoderm taxa (Taylor, 1978), and members of the genus *Charonia* within the Cymatiidae feed on echinoids, asteroids and holothurians (Kisch, 1952; McPherson, 1968; Work, 1969; Laxton, 1971; Percharde, 1972; Endean, 1973; Thomassin, 1976). Cymatiid phylogeny is not sufficiently well known for firm conclu-

sions to be drawn on the origin of echinoderm diets. Phylogenetically more 'primitive' recent cymatiids, however, feed on a variety of phyla and it is possible that a specialized diet on echinoderms is not a primitive characteristic. The phylogenetic relationship between the Cassidae and Cymatiidae is obscure, precluding meaningful speculation on the evolution of the cassid feeding method (Taylor, personal communication). Sohl (1969) published a photograph of the fossil burrowing echinoid *Hamea alta* (Arnolde & Clarke) with a hole in the test that was clearly made by a cassid, and this late Eocene fossil appears to be the earliest known record of cassid feeding activities.

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REFERENCES CITED

ABBOTT, R. T., 1968a, Helmet shells of the world (Cassidae): 1. *Indo-Pacific Mollusca,* 2: 7–201.

ABBOTT, R. T., 1968b, *Seashells of North America. A guide to field identification.* Golden Press, New York, 280 p.

ASANO, M. & ITOH, M., 1960, Salivary poison of a marine gastropod, *Neptunea arthritica* Bernardi, and the seasonal variation in its toxicity. *Annals of the New York Academy of Science,* 90: 674–688.

BAKUS, G. J., 1973, The biology and ecology of tropical holothurians. In: JONES, O. A. & ENDEAN, R. (eds.), *Biology and geology of coral reefs,* 2 Biology 1: 325–367. Academic Press, London.

BEU, A. G., HENDERSON, R. A. & NELSON, C. S., 1972, Notes on the taphonomy and paleoecology of New Zealand Tertiary Spatangoida. *New Zealand Journal of Geology and Geophysics,* 15: 275–286.

CARRIKER, M. R., 1978, Ultrastructural analysis of dissolution of shell of the bivalve *Mytilus edulis* by the accessory boring organ of the gastropod *Urosalpinx cinerea. Marine Biology,* 48: 105–134.

CARRIKER, M. R. & WILLIAMS, L. G., 1978, The chemical mechanism of shell dissolution by predatory boring gastropods: a review and an hypothesis. *Malacologia,* 17: 143–156.

CARRIKER, M. R., WILLIAMS, L. G. & VAN ZANDT, D., 1978, Preliminary characterisation of the secretion of the accessory boring organ of the shell-penetrating muricid gastropod *Urosalpinx cinerea. Malacologia,* 17: 125–142.

CHESHER, R. H., 1969, Contributions to the biology of *Meoma ventricosa* (Echinoidea: Spatangoida). *Bulletin of Marine Science,* 19: 72–110.

CORNMAN, I., 1963, Toxic properties of the saliva of *Cassis. Nature,* 200: 88–89.

DAY, J. H., 1969, Feeding of the cymatiid gastropod, *Argobuccinum argus,* in relation to the structure of the proboscis and secretions of the proboscis gland. *American Zoologist,* 9: 909–916.

DAY, J. H., 1974, *A guide to marine life on South African shores,* Balkema, Cape Town and Rotterdam, iii + 300 p.

EDMUNDS, J. & EDMUNDS, M., 1973, Preliminary report on the Mollusca of the benthic communities off Tema, Ghana. *Proceedings of the Fourth European Malacological Congress; Malacologia,* 14: 371–376.

ENDEAN, R., 1969, *Report on investigations made into aspects of the current* Acanthaster planci *(crown of thorns) infestation of certain reefs of the Great Barrier Reef.* Fisheries Branch, Queensland Department of Primary Industries, Brisbane.

ENDEAN, R., 1972, Aspects of molluscan pharmacology. In: FLORKIN, M. & SCHEER, B. T., (eds.) *Chemical Zoology,* 7: Mollusca, p. 421—466. Academic Press, New York, London.

ENDEAN, R., 1973, Population explosions of *Acanthaster planci* and associated destruction of hermatypic corals in the Indo-West Pacific region. In: JONES, O. A. & ENDEAN, R. (eds.), *Biology and geology of coral reefs,* 2: Biology 1: 389–438. Academic Press, London.

FÄNGE, R. & LIDMAN, U., 1976, Secretion of sulfuric acid in *Cassidaria echinophora* Lamarck (Mollusca: Mesogastropoda, marine carnivorous snail). *Comparative Biochemistry and Physiology,* 53A: 101–103.

FOSTER, R. W., 1947, *Cassis tuberosa* L. feeding on an echinoid (*Clypeaster rosaceus* L.). *Nautilus,* 61: 35–36.

GLADFELTER, W. B., 1978, General ecology of the cassiculoid urchin *Cassidulus caribbearum* [sic]. *Marine Biology,* 47: 149–160.

GRANGE, K. R., 1974, The feeding of *Tonna ceverisina*. *Poiriera,* 7: 57–61.

HENDLER, G., 1977, The differential effects of seasonal stress and predation on the stability of reef-flat echinoid populations. *Proceedings Third International Coral Reef Symposium,* 1 Biology: 217–223.

HOUBRICK, J. R. & FRETTER, V., 1969, Some aspects of the functional anatomy and biology of *Cymatium* and *Bursa*. *Proceedings of the Malacological Society of London,* 38: 415–429.

HUGHES, R. N., 1980, Optimal foraging theory in the marine context. *Oceanography and Marine Biology: an Annual Review,* 18: 423–481.

HUGHES, R. N. & HUGHES, H. P. I., 1971, A study of the gastropod *Cassis tuberosa* (L.) preying upon sea urchins. *Journal of experimental marine Biology and Ecology,* 7: 215–315.

KISCH, B. S., 1952, Further note on *Charonia lampas* (L.). *Journal of Conchology,* 23: 266.

LAXTON, J. H., 1971, Feeding in some Australasian Cymatiidae (Gastropoda: Prosobranchia). *Zoological Journal of the Linnaean Society,* 50: 1–9.

LYMAN, F. B., 1937, Food of *Cassis madagascariensis*. *Nautilus,* 51: 34.

MCPHERSON, B. F., 1968, Contributions to the biology of *Eucidaris tribuloides* (Lamarck). *Bulletin of Marine Science,* 18: 400–443.

MOORE, D. R., 1956, Observations of predation on echinoderms by three species of Cassidae. *Nautilus,* 69: 73–76.

NÜSKE, H., 1973, Cytologische Untersuchungen an der Sauredruse der Meeresschnecke *Cassidaria echinophora*. *Cytobiologie,* 7: 164–180.

PANCERI, P., 1869, Gli organi e la secrezione dell'acido solforico nei gasteropodi. *Atti dell'Academia delle scienze fisiche e matematiche, Napoli,* 4: 1–56.

PERCHARDE, P. L., 1972, Observations on the gastropod *Charonia variegata* in Trinidad and Tobago. *Nautilus,* 85: 84–92.

PROFANT, R. J., 1970, Reef wreckers. *Tabulata,* January 1, 1970: 3–5. (Santa Barbara Malacological Society, Santa Barbara).

REYNELL, A., 1905, Some account of the anatomy of *Cassidaria rugosa* (Linn.). *Proceedings of the Malacological Society of London,* 6: 292–299.

SCHROEDER, R. E., 1962, Urchin killer. *Sea Frontiers,* 8: 156–160.

SNYDER, N. & SNYDER, H., 1970, Alarm response of *Diadema antillarum*. *Science,* 168: 276–278.

SOHL, N. F., 1969, The fossil record of shell boring by snails. *American Zoologist,* 9: 725–734.

TAYLOR, J. D., 1978, Habitats and diet of predatory gastropods at Addu Atoll, Maldives. *Journal of experimental marine Biology and Ecology,* 31: 83–103.

TAYLOR, J. D., MORRIS, N. J. & TAYLOR, C. N., 1980, Food specialization and the evolution of predatory prosobranch gastropods. *Palaeontology,* 23: 375–409.

THOMASSIN, B. A., 1976, Feeding behaviour of the felt-, sponge-, and coral-feeder sea stars, mainly *Culcita schmideliana*. *Helgoländer wissenschaftliche Meeresuntersuchungen,* 28: 51–65.

WEBER, H., 1927, Der Darm von *Dolium galea* L., eine vergleichende anatomische Untersuchung unter besonderer Berucksichtigung der *Tritonium*-arten. *Zeitschrift für wissenschaftliche Biologie,* Abt. A, *Zeitschrift für Morphologie und Ökologie der Tiere,* 8: 663–804.

WORK, R. C., 1969, Systematics, ecology and distribution of the mollusks of Los Roques, Venezuela. *Bulletin of Marine Science,* 19: 614–711.

YANINEK, J. S., 1978, A comparative survey of reef-associated gastropods at Maziwi Island, Tanzania. *Journal of the East African Natural History Society and National Museum,* 31: 1–16.